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Longevity of flowers in the rattans *Calamus subinermis* and *C. caesius* (*Palmae : Calamoideae*)

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Summary. The development of the flowers from opening to senescence and fruit formation was observed in three female inflorescences and one male inflorescence of *Calamus subinermis*, and two female inflorescences and six male inflorescences of *C. caesius* in the Sandakan Residency, Sabah. In the male flowers of both species the longevity was found to be 6–12 hours, and anthesis occurred at night. The behaviour of the acolyte (sterile male) flowers on the female inflorescences was the same as the fertile males, except that no pollen was produced. The development of the female flowers from emergence to senescence and shrivelling of the stigmas took 5 days in *C. subinermis* and 10 days in *C. caesius*. The receptivity of the stigmas, as determined by the peroxidase test, and artificial pollination followed by bagging, was about 2 days in *C. subinermis* and about 4 days in *C. caesius*. Low light intensity and high relative humidity extended the stigma receptivity for 1–2 days. The implications of these observations on natural and controlled pollination are discussed.

The genus *Calamus* is dioecious, with separate male and female plants. During a flowering season, each sexually mature stem produces from one to four inflorescences which are usually borne at consecutive leaf axils. The female inflorescence branches to the second order, and the flowers are borne in pairs (or dyads) of female and sterile male (or acolyte) flowers on both sides of the rachillae. The male inflorescence

branches to the third order, and the male flowers are arranged singly, but occasionally in pairs, long both sides of the rachillae.

The longevity of a flower has been defined by Primack (1985) as the length of time an individual flower remains open in the field with a fresh-appearing perianth, stigma and/or stamens. This definition is followed in this paper, except that in the male flowers, pollen grains are released from the opening to abscission of the flowers, and their longevity is considered to be the duration between opening and abscission. Previous reports on the pollination biology of rattan have been based on static observations (e.g., Dransfield 1979, Madulid 1980, Kiew & Muid 1989); the longevity of rattan flowers is thus not known. To determine the longevity of the male flowers and the duration of stigma receptivity of two important indigenous *Calamus* species in Sabah, *C. subinermis* H. Wendl. *ex* Becc. (locally known as *rotan batu, rotan tunggal* or *bangkavazan*) and *C. caesius* Bl. (locally known as *rotan sega*), this study was carried out. *C. subinermis* occurs naturally on coastal dryland forests. *C. caesius* is usually found on alluvial flats, seasonally flooded riverbanks and the margins of freshwater or peat swamps. Knowledge of the longevity and the duration of stigma receptivity of the flowers is important for an understanding of natural pollination and for carrying out controlled pollination in breeding programmes.

Materials and methods

Three female inflorescences from different planted stems of *C. subinermis* in the Sepilok Arboretum were selected for the study from January to August, 1994. These stems had crowns exposed to different light conditions (estimated with a spherical densiometer to be about 20, 40 and 80% of the open, respectively) and in different health (Table 1). Ten to 30 female flowers in each inflorescence were tagged. The development of these and the sterile male flowers was recorded at 24 hours intervals

Table 1. Stems of *Calamus subinermis* in the Sepilok Arboretum chosen for investigation of stigma receptivity.

Stem No.	Stem Length (m)	Exposure of Crown (% of Open)	Condition of stem
1A	20	20	Vigorous, healthy
21A	40	80	Vigorous, healthy
21C	30	40	Broken apex, unhealthy

until the stigmas had turned brown/black or the flowers had aborted. The stages (a–h in Fig. 1) of development of the female flowers were recorded.

Pollen collected from a male inflorescence of *C. subinermis* in Kolapis A (situated about 40 km west of Sepilok) was applied to the stigmas of the female flowers at the various stages of development with a camel hair brush. The pollen was confirmed to be viable by *in vitro* assay with Brewbaker's pollen germination medium as described by Lee & Jong (1995). Some of the rachillae which bore the artificially pollinated flowers were then enclosed in bags made of white cotton cloth with a mesh size smaller than the rattan pollen grain (about 15–25 μm). Two to four bagged rachillae were not artificially pollinated to serve as the control. When the stigmas of the flowers had turned brown, the bags were removed. As no male inflorescences of *C. subinermis* in the Arboretum and within a radius of 25 km from the Arboretum underwent anthesis during the study period, it was not necessary to bag the flowers to exclude pollen prior to anthesis. The number of intact flowers was recorded at 24 hours intervals for 4–6 days, followed by 48 hours intervals for 8 days. Thereafter, observation on the number of developing young fruits was carried out at weekly intervals for four weeks, then fortnightly for two months and monthly until the fruits reached maturity. The original number of pollinated flowers per rachilla ranged from 30 to 48 in stems no. 21A and 21C and from 20 to 30 in stem no. 1A.

The stigmas at the different stages of development were also tested for the presence of peroxidase by immersing them in a 3% aqueous hydrogen peroxide solution. Effervescence indicates the presence of the enzyme which is normally abundant in receptive stigmas (Dafni 1992).

Observation on the anthesis and longevity of the fertile male flowers and sterile male (acolyte) flowers was carried out on one male inflorescence and one female inflorescence of *C. subinermis* in a natural stand in Berhala Island and the Sepilok Arboretum respectively in September, 1991. The time and duration of opening of the petals, dehiscence of the anthers and the senescence of these flowers were recorded. Observation on the flowers during a subsequent study on the nocturnal pollinators in September, 1993, confirmed these observations.

The study on the floral biology of *C. caesius* was carried out similarly. However, owing to the less frequent flowering in this species (once a year, compared with twice a year in *C. subinermis*) and the lack of accessible mature plants, only two female inflorescences on one stem in the Sepilok Arboretum were studied in October, 1993. It was possible to carry out observation on the male inflorescences on 4 stems in the Sepilok Arboretum and 2 stems in Kolapis A. The peroxidase test for stigma receptivity was carried out as in *C. subinermis*.

All of the study sites are situated within the Sandakan Residency.

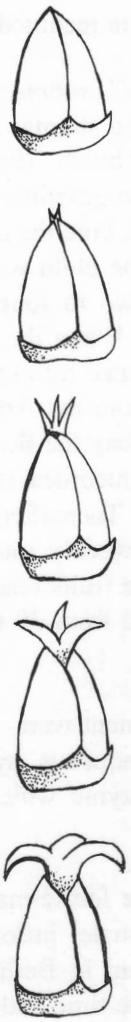

Fig. 1. Stages of development of female flowers of *Calamus subinermis* and *C. caesius*.
In stages b–e, the stigma lobes are yellow and shiny.

Stage a : Flower bud turns yellow; stigma is not visible.
Stage b : Stigma starts to protrude out.
Stage c : Stigma lobes elongate but are still straight.
Stage d : Stigma lobes start to curve.
Stage e : Stigma has reached maximum size.

In stages f to h, the shape of stigma is the same as stage e.

Stage f : Colour of the stigma lobes is brownish yellow.
Stage g : Colour of stigma is yellowish brown.
Stage h : Colour of stigma is dark brown/black.

Results

Calamus subinermis

General

About two to four days prior to the opening of female, sterile male and fertile male flowers, the colour of the sepals and petals changed from green to yellow. One or two days before the opening of the flowers, nectar exuded from between the petals and sepals. From visual estimation, nectar production reached the maximum when the flowers opened. The production of nectar was accompanied by the emission of fragrance, the intensity of which appeared to roughly correspond to the amount of nectar produced. Anthesis lasted for 10–15 days in an inflorescence in both sexes.

Male and sterile male flowers

Male flowers generally opened between 6 and 8 pm. The whole process of opening from the splitting of the flower bud to the formation of a fully opened flower took about 20 minutes. After the splitting of the bud, the introrse anthers were exposed and dehisced to release the pollen. Following anthesis and when most of the pollen had been shed, the flowers shrivelled and fell off between midnight and 6 am. Thus the longevity of the male flowers was about 6–12 hours.

The behaviour of the sterile male flowers on the female inflorescences during anthesis was the same as the fertile males, except that no pollen was produced by the staminodes which bore empty anthers.

Female flowers

The duration of the different stages of development of the female flower was as follows:

Stage a to stage c	:	1 day
Stage c to stage e	:	1 day
Stage e to stage f	:	1 day
Stage f to stage g	:	1 day
Stage g to stage h	:	1 day
Total	:	5 days

The elongation of the stigmas took place mainly at night. Low light intensity and high relative humidity, as were found when the rachillae were bagged extended the

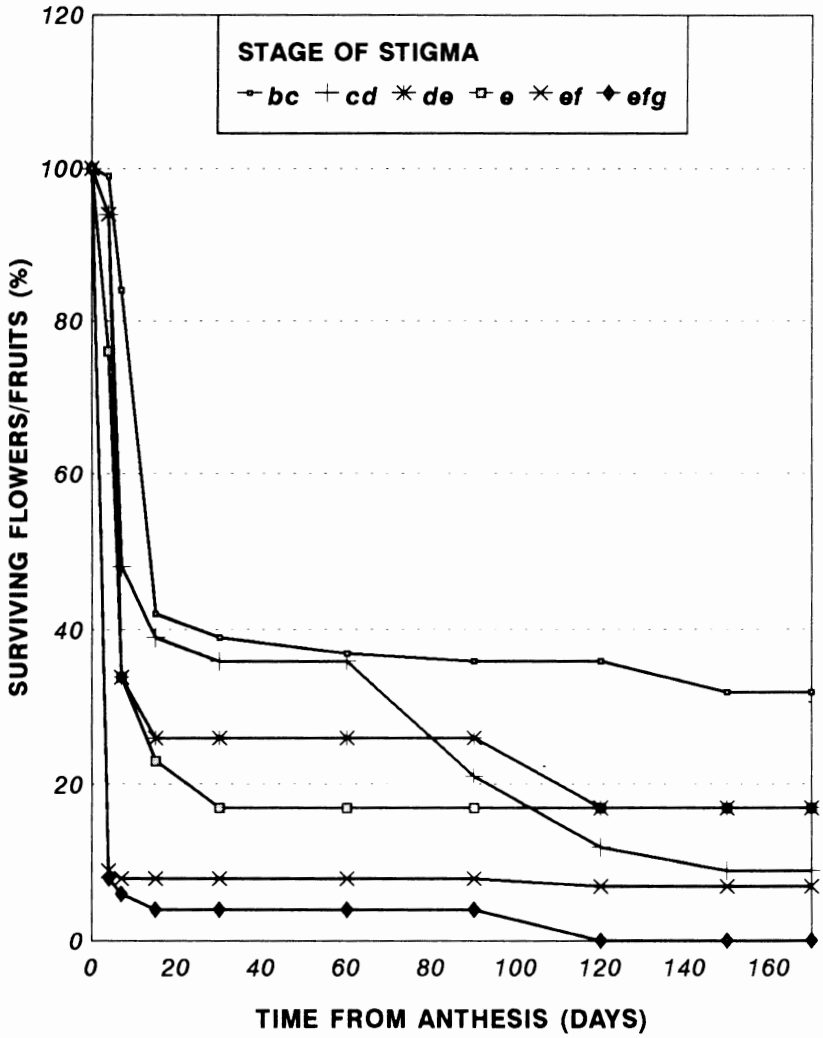

Fig. 2. Change in % of intact female flowers/fruits with time after controlled pollination of flowers at different stages of anthesis (Stages a–h shown in Fig. 1) in an inflorescence of *Calamus subinermis* on stem no. 21A of Table 2. Further explanation in text.

duration of development of the stigmas from stage a to stage f by one to two days. No difference in the duration of development of the stigmas from stage a to stage f was observed between the pollinated and unpollinated flowers.

The results of the artificial pollination experiment (Table 2 and Fig. 2) show that the stigmas at stages b to e were receptive, as pollination at these stages led to the production of mature fruits. The average proportion of flowers which were pollinated at these stages and developed into mature fruits in the three inflorescences was about 21%. The observed deviation from this average value was random; that is, pollination at none of these stages of stigma development consistently led to highest fruit set. This was confirmed by response curve analysis of the percentage of the pollinated flowers on the rachillae which developed into ripe fruits by the stage of development of the rachillae. The rachillae with flowers at stages b and c, c and d, d, and e were considered to be at levels 1, 2, 3 and 4, respectively, in the analysis. The linear, quadratic and cubic components of the response curve were found to be not significant ($p>20\%$). Pollination carried out from stage f onwards did not result in fruit production, and flowers thus pollinated aborted within three weeks. Hence the duration of stigma receptivity was 2 days in high light intensity in the open and 3–4 days in low light intensity and high relative humidity. When the stigmas were receptive, copious stigmatic fluid was produced, indicating that they are of the "wet" type (Dafni 1992).

The peroxidase test shows that peroxidase was most abundant in the stigmas from stages b to e. Stigmas at stages f and g still contained peroxidase but its activity was greatly reduced. This result is consistent with the failure of fruit set in the artificial pollination experiment.

The unpollinated female flowers (both bagged and unbagged) in this study all aborted, indicating that agamospermy does not occur in the species. This result differs from an earlier observation that in the isolated female stem (no. 21A), fruits developed parthenocarpically or stenospermocarpically (i.e., development of fruits after degeneration of fertilized ovules) but contained no seed (Lee, unpublished data).

Table 2 also shows that ripe fruits were formed fastest (170 days) in the inflorescence on stem no. 21A growing vigorously under about 80% canopy opening, followed by stem 1A (180 days) growing vigorously under about 20% canopy opening. The longest fruit maturation time was in stem 21C with a defective shoot and under about 40% canopy opening.

Calamus caesius

The development of the flowers of *C. caesius* (Fig. 3 and 4) was the same as that of *C. subinermis*, except that the longevity of the female flowers of the former was about

Table 2. Percentage of intact female flowers/fruits after controlled pollination of flowers at different stages of anthesis (Stages a-h shown in Fig. 1) in three inflorescences of *Calamus subinermis* in the Sepilok Arboretum in 1994. Pollination after stage e did not result in fruit set. The last column with survival % for each of the three inflorescences shows the time since pollination for the formation of ripe fruits, which differed among the three stems under different light intensity and in different health.

Inflorescence on Stem No	Rachilla No.	of Flowers	Time after Controlled Pollination (Days) 4	7	15	30	60	90	120	150	170	180	210
	2			0	0	0	0	0	0	0	0		
21A	3	ef	4	4	4	4	4	4	2	2	2	Fruits	
	4	efg	8	6	4	4	4	4	0	0	0		
	5	ef	13	11	11	11	11	11	11	11	11	had	
	6	e	86	50	33	33	33	33	33	33	33		
	7	e	66	18	13	11	11	11	11	11	11	ripened	
	8	de	94	34	26	26	26	26	17	17	17		
	9	cd	94	48	39	36	36	21	12	9	9		
	10	bc	100	79	47	45	42	42	42	34	34		
	11	abc	97	74	33	30	27	27	27	24	24		
	12	abc	100	100	46	41	41	38	38	38	38		

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(Table 2 continued)

Inflorescence on Stem No	Rachilla No.	of Flowers	Time after Controlled Pollination (Days) 4	7	15	30	60	90	120	150	170	180	210
	1	fg	0	0	0	0	0	0	0	0	0		0
	2	fg	0	0	0	0	0	0	0	0	0		0
21C	3	ef	7	0	0	0	0	0	0	0	0		0
	4	ef	42	8	3	0	0	0	0	0	0		0
	5	ef	36	10	0	0	0	0	0	0	0		0
	6	de	64	44	28	28	26	23	23	21	21		18
	7	de	86	75	64	58	47	31	28	28	28		28
	8	cd	61	52	48	48	33	24	24	24	24		24
	9	bc	79	68	68	68	38	29	21	21	21		21
	10	a	53	47	19	19	19	9	9	9	9		9
	1	fg	15	4	0	0	0	0	0	0		0	
1A	2	efg	30	15	11	4	0	0	0	0		0	Fruits
	3	ef	48	33	33	15	0	0	0	0		0	
	4	ef	67	52	48	26	0	0	0	0		0	had
	5	e	81	70	63	41	22	19	19	19		19	
	6	cd	78	63	56	26	26	22	22	22		22	ripened
	7	bc	93	74	67	30	22	15	15	15		15	
	8	ab	100	74	63	22	19	15	15	15		15	

Fig. 3. Male flowers of *Calamus caesius* in Sepilok.

Fig. 4. A female rachilla of *Calamus caesius* in Kolapis A.

twice that of the latter and that the duration of anthesis of the inflorescence was longer, i.e., 15–20 days. The duration of the different stages of development of the female flowers in an inflorescence under medium light intensity (30% canopy opening) under the forest canopy was as follows:

Stage a to stage b	:	1 day
Stage b to stage d	:	1 day
Stage d to stage e	:	1 day
Stage e to stage f	:	2 days
Stage f to stage g	:	2 days
Stage g to stage h	:	3 days
Total	:	10 days

As in *C. subinermis*, low light intensity and high relative humidity extended the duration of stigma receptivity by one to two days, and there was no difference in the duration of development of the stigmas from stage a to stage f between the pollinated and unpollinated flowers. The stigmas are also of the "wet" type.

The controlled pollination experiment did not yield any conclusive result because the partial inflorescences tagged for this study were damaged by a large fallen branch when the fruits were still very young, and the experiment has not been repeated. However, judging from the similarity in the behaviour and morphology of the flowers of this species and that of *C. subinermis*, as well as the result of the peroxidase test, it is concluded that the female flowers are also receptive during stages b to e.

In the male flower, anthesis mostly occurred between 6 and 9 pm, and senescence and abscission between midnight and 6 am. Its longevity is thus similar to that of *C. subinermis*.

Discussion and conclusions

The longevity of 6–12 hours in the male flowers of *C. caesius* and *C. subinermis* and the nocturnal anthesis observed in this study indicates that pollination mostly occurs at night. The nocturnal pollination vectors are mostly noctuid and pyralid moths (Lee *et al.* 1995). However, as pollen viability is still substantial (>10%) 24 hours after anthesis (Lee & Jong 1995) and the duration of stigma receptivity in *C. subinermis* and *C. caesius* is 2 and 4 days respectively, the diurnal flower visitors such as trigonid bees and flies, which visit both intact and fallen flowers, also play a role, perhaps a minor one, in pollination (Lee *et al.* 1995).

In controlled pollination in breeding programmes, pollen should be collected between dusk and 9 pm. Pollen grains should be applied to the receptive stigmas at stages b to e. However, the relative effectiveness of diurnal and nocturnal pollination in producing seeds is not known.

The higher longevity observed in the female flowers compared with the males is consistent with the trend reported by Primack (1985) that female flowers last longer than the males in angiosperms. He argued that male flowers are shorter-lived probably because their usefulness is over as soon as the pollen is shed and that female flowers are adapted to remain receptive until compatible pollen has reached the stigma.

Flowers are a drain on the water and stored nutrients of the plant, as a result of transpiration and respiration (Nobel 1977). The extension of the receptivity of the stigma in both pollinated and unpollinated flowers by bagging, which reduces the light intensity, increases the relative humidity and possibly reduces the temperature of the lax inflorescence, supports the physiological argument (Primack 1985) for short longevity of flowers based on the need to reduce transpirational water loss and metabolic costs.

In many species, e.g., tropical orchids, flowers are long-lived in the absence of pollination, but senescence occurs rapidly after pollination (Arditti 1979). This has been interpreted as an adaptation to promote visitation to the unpollinated flowers (Gori 1983). The similarity in the duration of stigma development from stage a to stage f in the pollinated and unpollinated female flowers observed in this study is probably because such an adaptation is absent in these relatively short-lived flowers, or the interval of observation (24 hours) is too long to detect the post-pollination senescence of the stigmas.

The abortion of unpollinated female flowers in *C. subinermis*, in contrast to an earlier observation that the same isolated female stem parthenocarpically (or stenospermocarpically) produced fruits which contained no seed, indicates that parthenocarpy or stenospermocarpy in the species is probably the result of genetic interaction with the environment. The trigger for parthenocarpy or stenospermocarpy, possibly the physiological state of the plant (e.g. sufficient food reserve) in response to environmental stimuli, has yet to be investigated. Stenospermocarpy might have occurred after self-fertilization, as the acolyte and pistillate flowers on female inflorescences of *C. subinermis* have been observed to produce viable pollen (Lee, unpublished data).

The similarity in the behaviour between the acolyte flowers on the female inflorescence and the fertile male flowers implies that the former's role in pollination is probably by serving as an olfactory and visual attractant, and by producing nectar as a reward for the pollinators.

The longevity of the female flowers of the two *Calamus* species investigated is comparable to that of two other locally widely cultivated palms, *Elaeis guineensis* (oil palm, 36–48 hours (Hartley 1988)) and *Cocos nucifera* (coconut; 3 days in tall palms, 2 days in dwarf palms (Ohler 1984)). In coconut, pollen is shed in bud and the staminate flowers open and absciss within two days (Ohler 1984). In oil palm, staminate anthesis has been reported for the whole inflorescence but not for individual flowers because abscission of male flowers in the pits formed by bracts is not apparent after anthesis. The flowers in a male inflorescence of oil palm usually open within two to four days, and shedding of pollen mostly occurs during the two to three days following the start of anthesis and stops within 5 days (Purseglove 1972). The longevity of the male flowers of these two species of palm is thus longer than that of *Calamus caesius* and *C. subinermis*.

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